

SEASONAL VARIATION IN INGESTION BY LARVAE OF *ENGRAULIS ENCRASICOLUS* AND OTHER FISH IN THE COASTAL WATERS OF ISRAEL

by

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ABSTRACT. - Clupeoid larvae (*Engraulis encrasicolus*, *Sardina pilchardus*, and *Sardinella aurita*) comprised 30 % of all fish larvae collected over 2 years at two stations in the coastal waters of Israel near Haifa. Growth rates of these species, determined by analysis of daily growth increments of otoliths, were used with Checkley's (1984) equation to calculate population ingestion rates. In 1984, as in 1985, the calculated ingestion rates were 10-20 % of annual primary production estimated from ^{14}C uptake. Because growth rates did not vary greatly with season, population ingestion rates followed closely the seasonal patterns in abundance of larvae, with maxima in late spring and in fall.

RÉSUMÉ. - Les larves de Clupeoidés représentent 30 % de la totalité des larves de poissons échantillonnées pendant deux ans dans deux stations côtières situées près de Haifa. Les coefficients de croissance déterminés par l'analyse de la croissance journalière des otolithes ont été utilisés, à l'aide de l'équation de Checkley (1984), pour calculer les coefficients d'ingestion de la population. En 1984, comme en 1985, les coefficients d'ingestion ainsi calculés représentent 10 à 20 % de la production primaire annuelle estimée d'après l'assimilation de Carbone 14. Comme les coefficients de croissance ne varient pas beaucoup pendant les différentes saisons, les coefficients d'ingestion de la population ont suivi de près les variations saisonnières en quantité de larves avec un maximum à la fin du printemps et un autre en automne.

Key-Words : Clupeoid, *Engraulis encrasicolus*, *Sardina pilchardus*, MED, Israel, Larval growth rate.

The presence of substantial numbers of larval fish in the southeastern Mediterranean is particularly interesting because of the extremely low primary production in these waters (Berman *et al.*, 1984). Not only is production low but also most of the production is by the picoplankton ($< 3\mu\text{m}$) size fraction. Food chain efficiency should therefore be low because of the increased number of trophic levels. However, in a previous study Walline (1987) calculated that in 1984 larval fish in these waters ingested $2.2 \text{ gC m}^{-2}\text{y}^{-1}$, which is approximately 10-20% of primary production estimated by ^{14}C techniques.

The apparent discrepancy could be accounted for if fish larvae were more abundant in 1984 than in other years. Reported here are the results from a second year of sampling, undertaken in an attempt to verify the calculated ingestion rates. The longer time series also makes it possible to examine seasonal trends in growth rate, abundance, and ingestion rates and to speculate about possible causes of the observed trends.

As in Walline (1987) the daily deposition of the observed growth increments is assumed in this study. However, there is now evidence confirming this assumption. Re (1984) found that the increments observed on the otoliths of *Sardina pilchardus* are deposited daily, and, using the same methods, has recently shown that otolith microgrowth increments are also deposited on a daily basis by *Engraulis encrasicolus* larvae (Re, in press).

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METHODS

Ichthyoplankton collections were made 13 times in two years at two stations west of the Israel Oceanographic Institute in Haifa, Israel. Station N was located 2 km offshore in water 30 m deep, and Station P was located 10 km offshore at the shelf break in waters 250 m deep. Based on the observations of Azov (1986), these stations were expected to differ substantially in phytoplankton standing stocks and production, and were chosen as representative of pelagic inshore and offshore waters, respectively. The sampling methods and techniques for analysis of growth rates and ingestion rates were identical to those reported previously (Walline, 1987). Sampling was done with a neuston net (Ben-Yami *et al.*, 1970) and with a 60 cm bongo net fitted with a flowmeter to estimate sample volumes.

Larval lengths were corrected for net shrinkage (10 min. estimated average time in the net) and for additional shrinkage after preservation using formulae presented by Theilacker (1980) for *Engraulis mordax*. Growth rates were calculated from larval lengths (corrected for shrinkage) and ages, which were determined using daily growth increment methods (Campana and Neilson, 1985). Ingestion rates were calculated using a *generalized* equation based on the relationship observed between directly measured ingestion and growth for a variety of fish species (Checkley, 1984). Checkley's equation gives ingestion rate as a function of growth rate and temperature. These data were used together with the abundance and length distribution of larval clupeoid fishes (sardines and anchovies) to calculate the population ingestion rate. The ingestion rate contribution from other species of fish was estimated by multiplying total numbers of fish larvae by the average ingestion per *Engraulis encrasicolus* larva in the sample.

RESULTS

In 1984 and 1985 the anchovy *Engraulis encrasicolus* were the most abundant larvae in the samples. Anchovies and sardines composed approximately 30 % of the larvae at both stations and in both years. The abundance of anchovy declined in 1985 at the offshore Station P (Fig. 1), but large numbers of *Sardinella aurita* in the samples from June 1985 more than compensated for the decrease. Clupeoid larvae were more abundant at Station P than at Station N.

At Station P two peaks of abundance were observed in each year, one in the late spring-early summer and one in fall. In 1985 maximum numbers occurred later in the season than they did in 1984. The pattern was slightly different at Station N where the spring maximum in the abundance of *Engraulis* larvae was not observed in 1985. In 1984 the periods of maximum abundance were out of phase at the two stations, while in 1985, they coincided (Fig. 1).

Larvae were larger on the average during the winter (December to February) than at other seasons (Fig. 1). In general, the average length of larvae was inversely related to abundance. At the estimated growth rates, larvae could grow 10-15 mm mo⁻¹ so the persistent occurrence of relatively small larvae (for example, during May to November 84) indicates spawning, either locally or a short distance "upstream". At the end of the fall season, small larvae no longer appeared, and average lengths increased dramatically.

Although growth rates of *E. encrasicolus* were not highly variable, small but significant differences were observed between stations and between years. Larvae grew faster at Station P than at Station N (0.53 and 0.47 mm d⁻¹ respectively, and faster in 1984 than in 1985 (0.55 and 0.46 mm d⁻¹ respectively). The additional data made it possible to compare growth rates from single sampling dates, subject to the limitations posed by the low numbers of *Engraulis* caught on some dates. The lowest growth rate, 0.30 mm d⁻¹, was observed in June 1984, 2 months after the abundance of anchovy larvae reached 53.4 m⁻², the maximum in the 2⁺ years of the study.

At Station P the seasonal pattern of food consumption by the population of anchovy larvae followed closely the pattern of abundance, while at Station N the fall season was

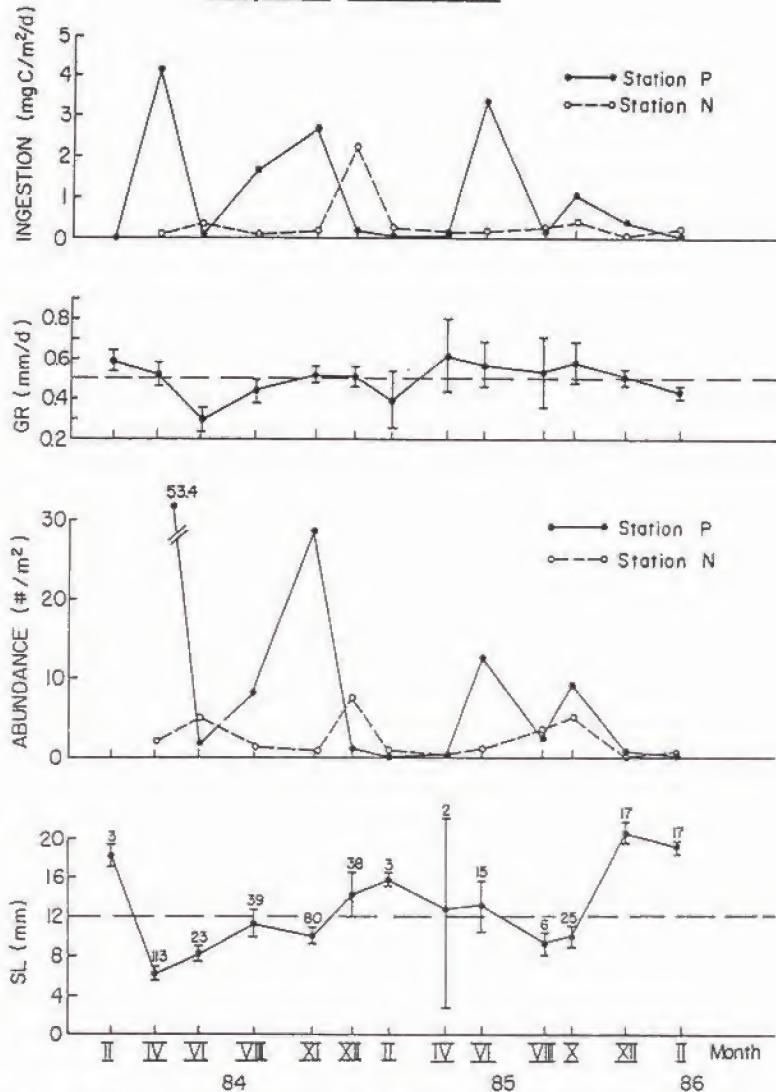


Fig. 1 : Population ingestion rate, average growth rate (GR), abundance and average length (SL) for *E. encrasicolus* on 13 sampling dates. Data from all stations and nets were combined to calculate GR and SL for each sampling date. Numbers above the error bars (+ 2 S. D.) indicate the number of larvae measured on the corresponding date for SL and GR.

relatively more important in terms of ingestion than in terms of abundance. In general, calculated ingestion was much lower at Station N due to lower abundances there. The differences in growth rates observed between the two stations had only a slight effect on the computed ingestion rates.

When consumption by *Sardinella aurita* and *Sardina pilchardus* is added to that of *E. encrasicolus*, the bimodality of the seasonal distribution of ingestion is emphasized (Fig. 2). Large numbers of *S. aurita* were present in June 1985, accounting for the relatively high rate

of ingestion observed then at Station N and the record high ($13.6 \text{ mg C m}^{-2} \text{ d}^{-1}$) observed at Station P. The occurrence of *S. pilchardus* accounted for most of the ingestion by clupeoid fish larvae in February 1986.

Fish larvae of other species (mainly stomiiformes, sparids, and mugilids) reach maximum abundances at the same times that numbers of clupeoid larvae are maximal. Thus, ingestion rates for all fish larvae combined reach maxima in the same seasons as ingestion by clupeoid larvae (Fig. 2). When clupeoid larvae constitute an unusually small fraction of the total numbers of fish larvae, the estimate of ingestion by all fish larvae is less reliable because the growth rates of those species were not measured. Rather, the total ingestion rate is based on the assumption that the ingestion rate of the *E. encrasicolus* larvae provides a good estimate of the ingestion rate for other species in the sample. Thus, the estimates of ingestion in the winter (the peak observed in Feb 86, for example) are not as reliable as those from spring and fall.

Average annual ingestion rates were nearly the same in 1985 as in 1984 (Table I). In both years ingestion at Station P was approximately 3 times that at Station N.

DISCUSSION

The 1985 results confirm those of 1984, especially with regard to the conclusion that either primary production supporting the food chain must be greater than the 40-50 $\text{mg C m}^{-2} \text{ d}^{-1}$ currently estimated from ^{14}C uptake data, or food consumption by the populations of larval fish must be overestimated by the techniques used in this study. The high annual rate of ingestion calculated for 1984 was not the result of anomalously high densities of fish larvae since an even higher annual consumption was observed in 1985.

The sampling frequency was not optimal since at the growth rates observed in the study, anchovy larvae can grow in a little over a month from a length of 5.7 mm at hatching to a size too big to be sampled adequately with the bongo nets. Theoretically, an important pulse of spawning could have occurred between sampling dates and gone more or less unnoticed. However, the seasonal distribution observed in 1984 was repeated so closely in 1985 that it seems unlikely. On the other hand, comparison of single months in the two years, for example Jun 84 and Jun 85, reveals that even though the seasonal pattern is sketched with a minimal sampling frequency, details are lost.

The results indicate that late spring and fall are the two periods of greatest larval abundance, and therefore, greatest demand on the food resources of larval fish in the coastal waters of Israel. The main spawning occurs at the end of the winter, just before stratification sets up. The situation appears on the surface to be similar to the classical one in temperate waters where the spring phytoplankton bloom begins as the mixed layer depth shallows to less than the compensation depth. However, because nutrients in the mixed layer of southeastern Mediterranean shelf waters are generally at extremely low levels even during winter, onset of stabilization does not cause a phytoplankton bloom. Azov (1986) reported occasional periods of high nutrient concentrations and associated phytoplankton blooms in the late winter at the two stations discussed here. He found that chlorophyll concentrations were highest at the end of winter. Since some time is necessary for these blooms to pass up the food chains to the level of larval fish food, the spring spawning could be timed to take advantage of increased densities of zooplankton which may follow these phytoplankton blooms.

The spawning by *Engraulis* and *Sardina* observed in the fall may be associated with periods of upwelling. Winds with N and NE components occur frequently at this transitional period of the year. Such winds drive surface waters offshore to be replaced by subsurface waters from farther offshore, i.e. upwelling. If the upwelled waters are relatively rich in nutrients, production will be stimulated (Townsend *et al.*, in press). Fall spawning may be timed to take advantage of increased zooplankton production.

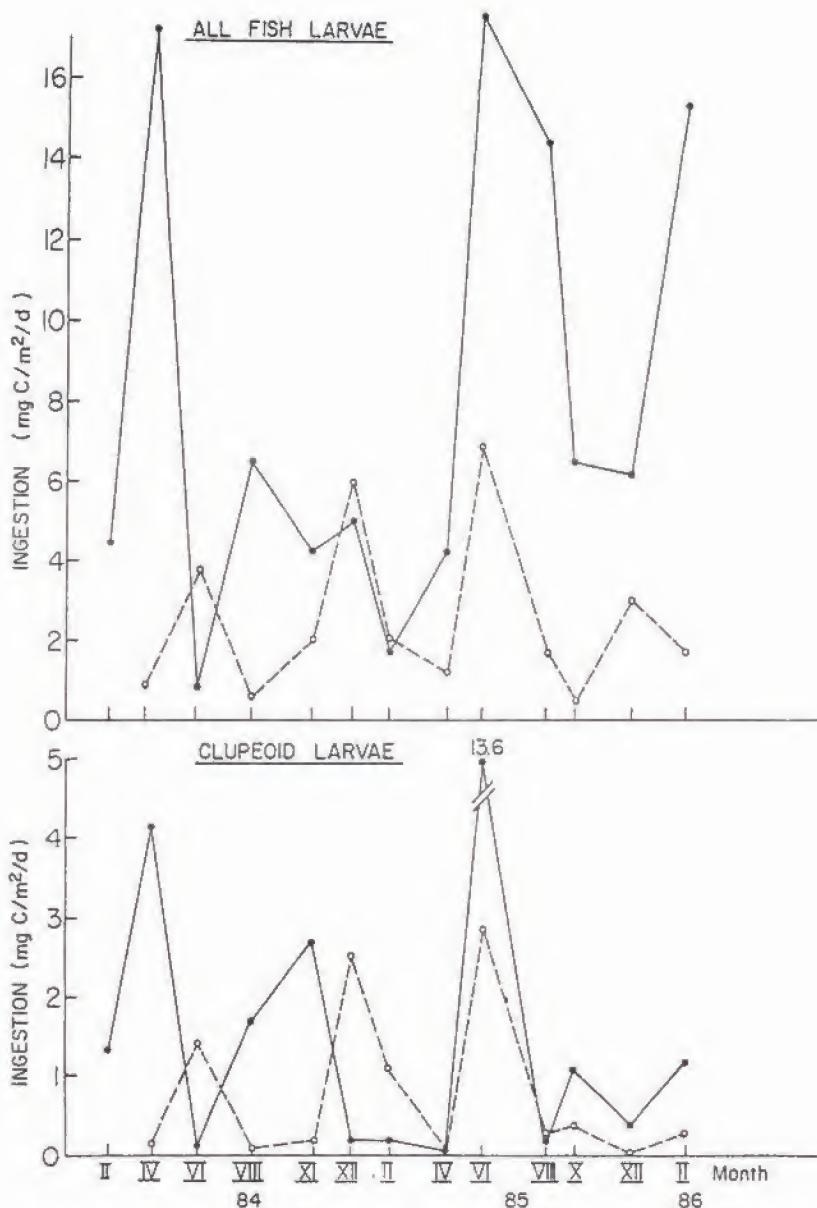


Fig. 2 : Ingestion rate on each of 13 sampling dates for populations of all fish larvae combined and for *E. encrasicolus*, *S. pilchardus*, and *S. aurita* combined, dotted line for Station N and solid line for Station P.

Table I : Average annual ingestion in $\text{gC m}^{-2} \text{y}^{-1}$.

Larval group	Sta.	Ing ('84)	Ing ('85)	Ing (Ave.)
<i>E. encrasicolus</i>	N	0.19	0.21	0.20
	P	0.54	0.31	0.42
All clupeoids	N	0.33	0.29	0.31
	P	0.62	0.95	0.79
All fish larvae	N	0.99	0.95	0.97
	P	2.34	3.07	2.70

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